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- limonite-stained white sandstone, 0.9 km (0.75 mi.) east of Lower Lake, 366 m (1200 ft.) S from bridge over Copsey Creek, in gully on W side of creek, SE 1/4 of NE 1/4 of section 11, T. 12 N, R. 7 W, U.S. Geological Survey, 7.5-minute, Lower Lake Quadrangle, 1975, Lake County, northern California. Martinez Formation. Age: Latest early Paleocene or earliest late Paleocene (uppermost "unnamed stage" or lowermost "Martinez Stage"). Collectors: D. W. Scharf & W. P. Popenoe. August 26, 1930.
- LACMIP 9936 [= LACMIP 28787]. Fossiliferous brown sandstone about 4.5 km (2.8 mi.) S of U.S. Highway 26, along west side of Bridge Creek, 610 m (2000 ft.) N and 805 (2640 ft.) E of SW corner of section 25, T. 13 S, R. 27 E, 44°24'34"N, 119°25'10"W, U.S. Geological Survey, 7.5-minute, Aldrich Mtn. North Quadrangle, 1972 (photorevised 1983), Grant County, east-central Oregon. Unnamed strata. Age: Earliest Late Cretaceous (Cenomanian Stage). Collectors: W. P. Popenoe and J. Alderson, June 12, 1975.
- LACMIP 10508. At approximately 404 m (1325 ft.) elevation, just below a coralline-algal interval in limey, muddy siltstone and west of small fault, in roadcut on north side of dirt road, on north slope of Trailer Canyon near top of ridge between Quarry and Trailer canyons, at approximately 50 m east of steel gate at boundary of Topanga State Park, and 4435 m (14,547 ft.) S and 5334 (17,496 ft.) W of NE corner of U.S. Geological Survey, 7.5-minute, Topanga Quadrangle, 1952 (photorevised 1981), east-central Santa Monica Mountains, Los Angeles County, southern California. Upper part of Santa Susana Formation. Age: Late Paleocene ("Martinez Stage"). Collectors: R. L. Squires and students, 1997.
- LACMIP 10676 [= CIT 1559]. Conglomeratic and fossiliferous outcropping in bed and banks of Los Banos Creek, 823 m (2700 ft.) N and 305 m (1000 ft.) W of SE corner of section 12, T. 11 S, R. 9 E, 36°59'28"N, 120°55'50"W, U.S. Geological Survey, 7.5-minute, Ortigalita Peak NW Quadrangle, 1969 (photorevised 1984), Merced County, north-central California. Moreno Formation, "Quinto Shale" member. Age: Late Cretaceous (Maastrichtian Stage). Collectors: B. C. Adams, R. W. Burger & L. Simon, circa 1942. [Locality is now at damsite of the Los Banos Reservoir.]
- LACMIP 10685 [= CIT 1573]. 975 m (3200 ft.) N and 549 m (1800 ft.) W of SE corner of section 12, T. 11 S, R. 9 E, 36°59'03"N, 120°55'58"W, U.S. Geological Survey, 7.5-minute, Ortigalita Peak NW Quadrangle, 1969 (photorevised 1984), Merced County, north-central California. Moreno Formation, "Quinto Shale" member. Age: Late Cretaceous (Maastrichtian Stage). Collectors: B. C. Adams & W. P. Popenoe, 1942. [Locality is now along the eastern side of the Los Banos Reservoir.]
- LACMIP 22536. See LACMIP 6298.

APPENDIX

LOCALITIES CITED

- CAS 183. See LACMIP loc. 6298.
- LACMIP 6297. In west bank of "Big Bend" of Cowlitz River, 590 m (1935 ft.) N and 375 m (1230 ft.) W of SE corner of section 28, T. 11 N, R. 2 W, U.S. Geological Survey, 15-minute, Castle Rock Quadrangle, 1953, about 2 km (1.2 mi.) E of Vader, Lewis County, southwestern Washington. Cowlitz Formation. Age: Late middle Eocene ("Tejon Stage"). Collectors: J. L. Goedert, 1982; R. L. Squires, July 13, 1988.
- LACMIP 6298 [= CAS 183, LACMIP 22536 (= UCLA 2536), UWBM 232, & UWBM 329]. Up-river from LACMIP loc. 6297, in west bank of "Big Bend" of Cowlitz River, 725 m (2378 ft.) N and 285 m (935 ft.) W of SE corner of section 28, T. 11 N, R. 2 W, U.S. Geological Survey, 15-minute, Castle Rock Quadrangle, 1953, about 2 km (1.2 mi.) E of Vader, Lewis County, southwestern Washington. Cowlitz Formation. Age: Late middle Eocene ("Tejon Stage"). Collectors: Numerous workers over the last 80 years or so.
- LACMIP 7047. A thin but richly fossiliferous layer of

- LACMIP 23348 [= UCLA 3348]. At elevation of 152 m (500 ft.), in light gray, fine-grained calcareous cemented arkosic sandstone, 30 to 60 cm thick, rich in molluscan fossils, in a small tributary (upper part of Well Canyon), north of Cañada Posa, 4325 m (14,190 ft.) N and 1737 m (5700 ft.) W of SE corner of U.S. Geological Survey, 7.5-minute, Santa Cruz Island A Quadrangle, 1943, southwestern Santa Cruz Island, Channel Islands, Santa Barbara County, southern California. Pozo Formation. Age: Late Paleocene ("Martinez Stage"). Collector: T. Rothwell, February 4, 1955.
- LACMIP 26720 [= UCLA 6720]. Hill with firebreak, 213 m (700 ft.) E of where 358 m (1175 ft.) contour line crosses Pulga Canyon, just below massive algal limestone beds, U.S. Geological Survey, 7.5-minute, Topanga Quadrangle, 1952 (photorevised 1981), Palisades Highlands, Santa Monica Mountains, Los Angeles County, southern California. Upper part of Santa Susana Formation. Age: Late Paleocene ("Martinez Stage"). Collector: J. Alderson, October, 1980.
- LACMIP 27083 [= UCLA 7083]. On a NW-facing hill-slope 7.1 km (4.4 mi.) ESE of Punta Rosarito and 0.9 km (0.6 mi.) E of Bahía Sebastian Vizcaino, southwestern Baja California Norte Mexico. Sepultura Formation. Age: Probably late Paleocene ("Martinez Stage"). Collector: A. J. C. Woods, circa 1975.
- SDSNH 3522. At elevation of 174 m (570 ft.), from a temporary excavation of approximately 7.5 m (24.6 ft.) of interbedded sandstone and muddy siltstone within a channel complex at the Laurels housing project, 372 m (1220 ft.) N and 665 m (2180 ft.) E of the SW corner of section 17, T. 12 S, R. 3 W, U.S. Geological Survey, 7.5-minute, San Marcos Quadrangle, 1968 (photorevised 1983), Laurels housing development project, west of the city of San Marcos, northern San Diego County, southern California. Santiago Formation. Age: Middle Eocene. Collector: D. J. McGuire, November 30, 1989.
- SDSNH 4105. From excavation on south side of California State Highway 78, in upper part of a medium dark gray, silty, fine-grained sandstone about 2.1 m (7 ft.) thick, about 3 km (1.86 mi.) SE of Sycamore Avenue, city of Vista, U.S. Geological Survey Quadrangle, 7.5-minute, San Marcos Quadrangle, 1968 (photorevised 1983), northern San Diego County, southern California. Santiago Formation. Age: Middle Eocene. Collectors: B. O. Riney and S. L. Walsh, August 12, 1996. [Excavation has been covered by backfilling of a new concrete retaining wall along south side of freeway.]
- UCR 4865. In roadcut on south side of California State Highway 78, 5.2 km (3.2 mi.) SE of city of Vista and 4.8 km NW of city of San Marcos, U.S. Geological Survey Quadrangle, 7.5-minute, San Marcos Quadrangle, 1968 (photorevised 1983), northern San Diego County, southern California. Santiago Formation. Age: Middle Eocene. Collector: C. R. Givens.
- UWBM 232. See LACMIP loc. 6298.
- UWBM 329. See LACMIP loc. 6298.

Review of the Genus *Actinocyclus* Ehrenberg, 1831 (Opisthobranchia: Doridoidea)

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Abstract. The genus *Actinocyclus* comprises two species, *Actinocyclus verrucosus* Ehrenberg, 1831, which is widespread through the tropical Indo-Pacific, from the Red Sea to Australia and Hawaii, and *Actinocyclus papillatus* (Bergh, 1878) known from East Africa, Papua New Guinea, the Philippines, and Japan. These two species are distinguishable by the external morphology and the arrangement and shape of the reproductive organs. There are no major radular differences. The genus name *Sphaerodoris* is a junior synonym of *Actinocyclus*. Other species names described within these two genera are either junior synonyms of *A. verrucosus* (*Sphaerodoris punctata* Bergh, 1878, *Sphaerodoris laevis* Bergh, 1890, *Sphaerodoris japonica* Eliot, 1913), synonyms of *A. papillatus* (*Sphaerodoris laevis* var. *variegata* Eliot, 1904), or belong to different genera (*Actinocyclus fragilis* Ehrenberg, 1831, *A. velutinus* Ehrenberg, 1831). *Aldisa nhatrangensis* Risbec, 1956, is also a junior synonym of *Actinocyclus verrucosus*.

INTRODUCTION

Gosliner & Johnson (1994) studied the phylogenetic relationships of the genus *Hallaxa* Eliot, 1909, and hypothesized that *Actinocyclus* Ehrenberg, 1831, was its sister taxon. According to these authors, *Actinocyclus* and *Hallaxa* are the only two members of the family Actinocyclusidae, which is the sister taxon to the Chromodorididae. At that point, the anatomy of *Actinocyclus* was known only from drawings of the reproductive system of *A. japonicus* by Kay & Young (1969) and Gosliner & Johnson (1994), and drawings of several radular teeth by Kay & Young (1969).

Up to now, several names have been proposed for species of this genus, but no one knows for sure how many valid species it comprises. Most authors appear to agree that *A. japonicus* is the valid name for a widespread Indo-Pacific species (Kay & Young, 1969; Bertsch & Johnson, 1981; Willan & Coleman, 1984; Wells & Bryce, 1993; Gosliner & Johnson, 1994), but its relationships with the type species, *A. verrucosus* Ehrenberg, 1831, from the Red Sea, are unknown.

The position of the Actinocyclusidae at the base of the Cryptobranchia makes this group essential for further understanding of the phylogenetic relationships within this diverse clade of dorids. Therefore, a more detailed knowledge of the anatomy of this taxon is critical for future research on the phylogeny of the Cryptobranchia.

In this paper I attempt a comprehensive anatomical study of the genus *Actinocyclus*, including features that might be important for future phylogenetic research, such as the central nervous system, the digestive system, and the reproductive system. In addition, a systematic review

of all species described is carried out in light of examination of specimens collected from several Indo-Pacific localities, trying to cover the entire geographic range of *Actinocyclus*. I also attempted to locate in several natural history museums the type material and other historically important specimens of all nominal species involved.

The material examined is deposited at the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ), the Museum für Naturkunde der Humboldt-Universität zu Berlin (MHUB), the Zoologisk Museum, Københavns Universitet, Copenhagen (ZMUC), and the Muséum National d'Histoire Naturelle, Paris (MNHN).

SYSTEMATIC DESCRIPTIONS

Genus *Actinocyclus* Ehrenberg, 1831

Actinocyclus Ehrenberg, 1831: [28]. Type species: *Actinocyclus verrucosus* Ehrenberg, 1831, by subsequent designation of J. E. Gray (1847).

Sphaerodoris Bergh, 1877:66. Type species: *Actinocyclus verrucosus* Ehrenberg, 1831, by monotypy.

Remarks: Ehrenberg (1831) introduced the new genus *Actinocyclus* based on two briefly described new species: *Actinocyclus verrucosus* and *A. velutinus*. A third species, *Actinocyclus fragilis*, was included with a question mark. Subsequently, J. E. Gray (1847) selected *Actinocyclus verrucosus* as the type species of *Actinocyclus*.

Bergh (1877) introduced the new genus *Sphaerodoris* based on *Actinocyclus verrucosus* Ehrenberg, 1831, including two new, not yet described species from the Philippines, and with a question mark "*Doris incii* (Alder)" [*Doris incii* J. E. Gray in M. E. Gray, 1850 is probably

a senior synonym of *Halgerda willeyi* Eliot, 1903 (S. Fahy, personal communication)]. Bergh (1877: 66–67) commented that *Actinocyclus* and *Sphaerodoris* are probably synonyms, but anatomical studies on *Actinocyclus* would be necessary to confirm this point. Since *Actinocyclus* was not anatomically studied, Bergh regarded this name as a synonym of *Sphaerodoris*. These sorts of decisions, which clearly violated the law of priority, were often taken by Bergh to suppress poorly described taxa. In any case, *Actinocyclus verrucosus* is the only valid nominal species originally and without doubt included in the genus *Sphaerodoris* Bergh, 1877, and therefore it is the type species by monotypy. Thus, *Sphaerodoris* is a junior objective synonym of *Actinocyclus*.

Eliot (1913) re-examined the holotype of *A. verrucosus* and confirmed that it belonged to the same genus as Bergh's species of *Sphaerodoris*. He also considered that *Actinocyclus* should be suppressed because of several contradictions between the original description and the actual specimen. On the contrary, O'Donoghue (1929) recognized that *Actinocyclus* is a valid genus and thus a senior synonym of *Sphaerodoris*. At the same time, he designated *Sphaerodoris punctata* as the type species of *Sphaerodoris*, but since this species was not included in the original description, such a designation is not valid. Since O'Donoghue's paper, most authors have accepted the name *Actinocyclus* as valid, and it is currently in common usage (Kay & Young, 1969; Bertsch & Johnson, 1981; Willan & Coleman, 1984; Wells & Bryce, 1993; Gosliner & Johnson, 1994).

Gosliner & Johnson (1994) reviewed the differences between *Hallaxa* and *Actinocyclus*. In light of phylogenetic analysis they concluded that these two genera are clearly distinguishable by the presence of two apomorphic features in *Actinocyclus*: "an elaboration of the anterior border of the foot and the presence of a secondary ampulla next to the hermaphroditic duct," and one apomorphic feature in *Hallaxa*: "presence of an elongate prostatic portion of the vas deferens." The present study confirms the presence of the elaboration of the anterior border of the foot and an unusual ampulla in *Actinocyclus*. In most groups of dorid nudibranchs the ampulla appears to be a dilatation of the hermaphroditic duct, whereas in species of *Actinocyclus* it is a lateral expansion. Even though the ampulla of *Actinocyclus* is arranged differently from that of other dorids, it seems to be a homologous structure and the term "secondary ampulla" appears not to be appropriate.

Actinocyclus verrucosus Ehrenberg, 1831

(Figures 1A,B, 2–4)

Actinocyclus verrucosus Ehrenberg, 1831:[28–29].

Sphaerodoris punctata Bergh, 1877:66 (*nomen nudum*).
Bergh, 1878:587–590, pl. 65, figs 1–5.

Sphaerodoris laevis Bergh, 1890:925–928, pl. 88, figs 3–12.

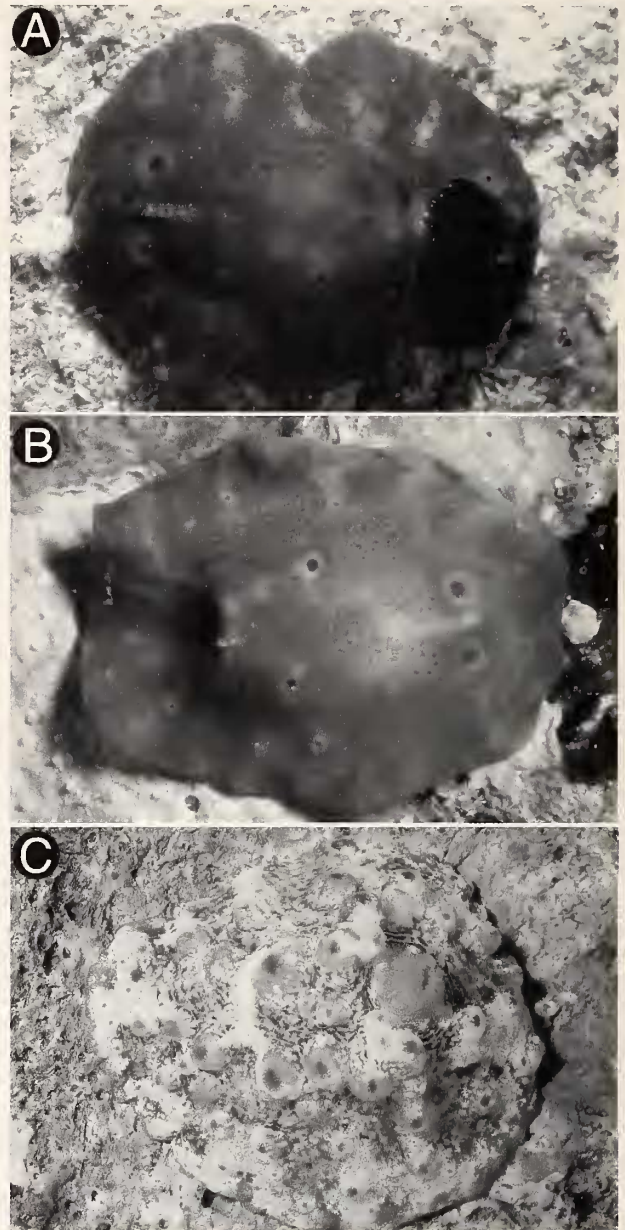


Figure 1. Living animals. A. Specimen of *Actinocyclus verrucosus* from Madagascar (CASIZ 073553), photo by T. M. Gosliner. B. Specimen of *A. verrucosus* from the Philippines (CASIZ 083843), photo by T. M. Gosliner. C. Specimen of *Actinocyclus papillatus* from Papua New Guinea (CASIZ 068651), photo by T. M. Gosliner.

Sphaerodoris japonica Eliot, 1913:23–26.

Aldisa nhatrangensis Risbec, 1956:14–15, pl. 20, fig. 109,
pl. 22, upper right figure.

Type material: *Actinocyclus verrucosus* Ehrenberg. Holotype (by monotypy): "Massaua" = Mits'iwa Island, Ethiopia, dissected (MHUB 594).

Sphaerodoris punctata Bergh. Holotype (by monoty-

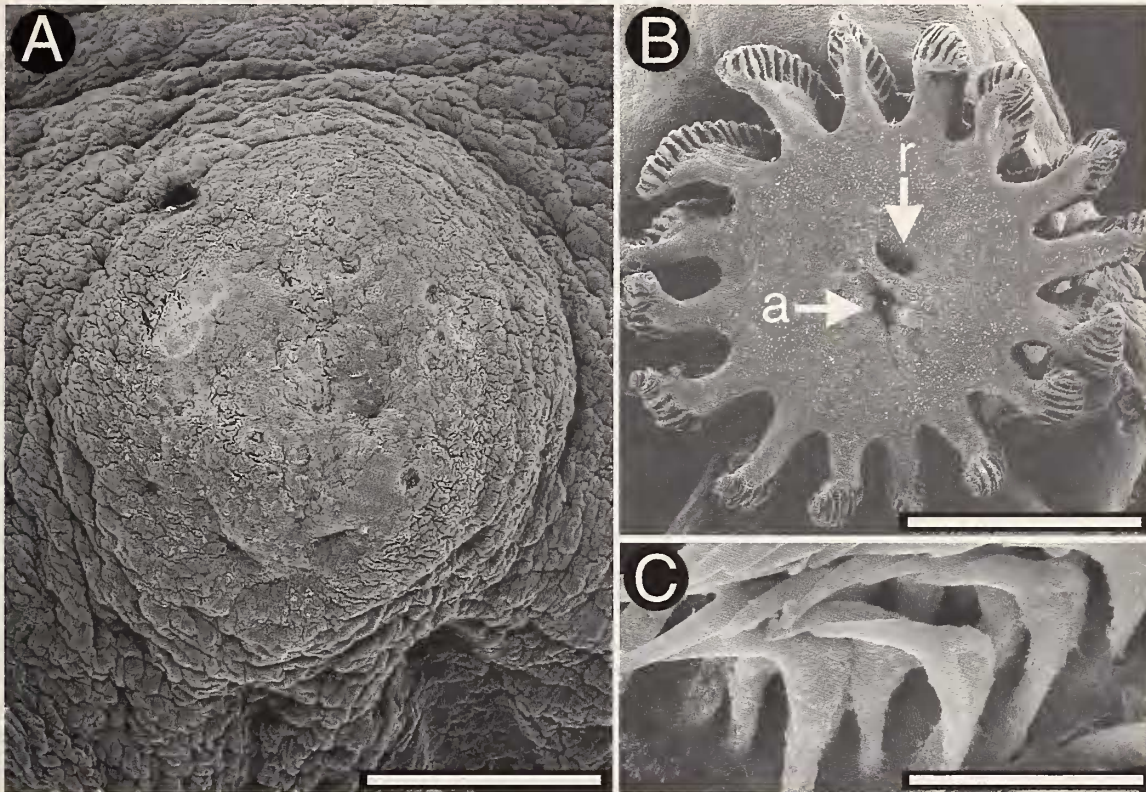


Figure 2. *Actinocyclus verrucosus*, scanning electron micrographs. A. Dorsal tubercle (CASIZ 099250), scale bar = 600 μm. B. Gill (CASIZ 086635), scale bar = 1.5 mm. C. Jaw elements (CASIZ 073553), scale bar = 15 μm. Abbreviations: a, anus opening; r, renal opening.

py): “Lapinig” probably Lapinin Island, Northwest of Bohol Island, Philippines, dissected (ZMUC GAS-2118).

Aldisa nhatrangensis Risbec. Holotype (by original designation): Hon Lon, Nha Trang, Vietnam, dissected (MNHN).

The type material of *Spaherodoris laevis* Bergh, and *Spaherodoris japonica* Eliot, is probably lost. No specimens are deposited at the Zoologisk Museum, Københavns Universitet, Copenhagen (K. Jensen, personal communication) or The Natural History Museum, London (A. Campbell, personal communication).

Additional material: South of Soanambo Hotel, Île Saint Marie, Madagascar, 6 April 1990, 1 specimen 18 mm preserved length, collected by T. M. Gosliner (CASIZ 073553). Devil’s Point, southwest side of Maricaban Island, Batangas, Luzon, Philippines, 19 February 1992, 1 specimen 21 mm preserved length, collected by T. M. Gosliner (CASIZ 083843); 19 February 1992, 1 specimen 39 mm preserved length, collected by T. M. Gosliner (CASIZ 083793); 17 March 1994, 1 specimen 20 mm preserved length, 24 m depth, collected by T. M. Gosliner (CASIZ 096290); 15 April 1996, 2 specimens 21 and 23 mm preserved length, 20 m depth, collected by T. M. Gosliner (CASIZ 106456). Okinawa, Ryukyu Islands, Ja-

pan, 2 May 1992, 1 specimen 23 mm long, dissected, collected by R. Bolland (CASIZ 086635). Tengan Pier, 14 km West of Ikei-shima, Okinawa, Ryukyu Islands, Japan, 9 April 1994, 1 specimen 35 mm preserved length, 12 m depth, dissected, collected by R. Bolland (CASIZ 099250), 18 October 1994, 1 specimen 33 mm preserved length, 12 m depth, collected by R. Bolland (CASIZ 104697). O Ennubuj, Kwajalein Atoll, Marshall Islands, 6 December 1992, 1 specimen 24 mm preserved length, 6 m depth, collected by S. Johnson (CASIZ 116662). Makua, Oahu Island, Hawaii, 17 April 1985, 1 specimen 12 mm preserved length, 5 m depth, collected by S. Johnson (CASIZ 116894).

Geographic range: This species is known from the Red Sea (Ehrenberg, 1831), East Africa (Eliot, 1904), Vietnam (Risbec, 1956), Japan (Eliot, 1913), the Philippines (Bergh, 1878), Indonesia (Bergh, 1890), Malaysia (Eliot, 1904), Western Australia (Wells & Bryce, 1993), Queensland (Willan & Coleman, 1984), and Hawaii (Kay & Young, 1969). The present paper reports the first records from Madagascar and the Marshall Islands.

External morphology: The body is elevated, short, oval, almost as long as wide (Figures 1A, B). The dorsum is

covered with several simple conical tubercles scattered irregularly. Some of them are much larger and have a depression on the apex (Figure 2A). The central part of the body is clearly elevated over the mantle margin, which is relatively narrow. The perfoliate rhinophores are composed of 20 lamellae in a 33 mm-long specimen (CASIZ 104697). There are 16 unipinnate branchial leaves in the 33 mm-long specimen (Figure 2B). In the living animal they are pointing inward, with the apices very close to each other.

The background color varies from cream brownish to dark brown or gray (Figure 1B). Some specimens are almost black (Figure 1A). There are paler areas, generally white or yellowish, irregularly distributed on the dorsum. The entire dorsum is covered with small, evenly distributed black spots. The depressions on the tips of the larger tubercles are dark brown or black. The gill is dark gray or black, with numerous small white spots, more densely distributed near the base. The rhinophores are the same color as the body.

The anterior border of the foot is not grooved or notched, with anteriorly directed foot margins partially surrounding the mouth area (Figure 3F). There are no oral tentacles.

Anatomy: The posterior end of the glandular portion of the oral tube has two strong retractor muscles (Figure 3D) which attach to the body wall. The oval, muscular buccal bulb has four additional muscles attached. Two long salivary glands connect with the buccal bulb at the sides of the esophageal junction. The buccal bulb is as long as the glandular portion of the oral tube. The jaws are composed of numerous undivided rodlets (Figure 2C). The radular formula is $65 \times 15.0.15$ in a 35 mm-preserved-length specimen (CASIZ 099250) and $70 \times 21.0.21$ in a 18 mm-preserved-length specimen (CASIZ 073553). Rachidian teeth are absent. The innermost lateral teeth are broad and thick (Figures 4A, B). They have a large rounded cusp and bear six to seven denticles along their inner edge. The mid-lateral teeth are narrow basally and elongated (Figure 4C). The outermost teeth are shorter than the mid-laterals (Figure 4D). The outer laterals bear 13–17 denticles along their inner margin. The esophagus is short and convoluted and connects with the digestive gland.

The narrow hermaphroditic duct expands into the elongate and convoluted ampulla, which inserts distally at the junction of the oviduct and the prostate (Figures 3B, C). The oviduct enters the female gland in the center of the mass. The prostate is rounded, as long as wide, and granular. It connects with a long duct that narrows and expands again into the short ejaculatory portion of the deferent duct. The muscular ejaculatory portion opens into a common atrium with the vagina. The penis is unarmed. The vagina is very long and undulate. Near its proximal end it joins the pyriform seminal receptacle, the uterine duct, and the oval bursa copulatrix. Both the bursa co-

pulatrix and seminal receptacle are stalked. The bursa copulatrix is about twice as large as the seminal receptacle (Figure 3C).

In the central nervous system (Figure 3E) the cerebral and pleural ganglia are partially fused and distinct from the pedal ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Paired gastroesophageal, rhinophoral, and optical ganglia are also present. The pedal ganglia are clearly separated. The pedal and parapetal commissures are fused together.

The circulatory system (Figure 3A) consists of a large heart and a single blood gland situated over the central nervous system.

Remarks: The original description of *Actinocyclus verrucosus* is a brief Latin text with no illustrations or anatomical information (Ehrenberg, 1831). The re-examination of the holotype of this species, collected Mits'iwa Island, Ethiopia, confirmed that its identity agrees with the usage of the name *Actinocyclus*. The specimen was dissected by Eliot during the preparation of his 1913 paper, the radula is missing, and the reproductive system is damaged. Yet, the external morphology is identical to that of our specimens.

Bergh (1877) introduced for the first time the name *Spaerodoris punctata*, but without description, and therefore it is a *nomen nudum*. Later, Bergh (1878) described this species based on preserved specimens from the Philippines. It is not possible to confirm their identity based on the original description of the external morphology; however, re-examination of the type material confirms that it is conspecific with *Actinocyclus verrucosus*. The 38 mm-long holotype of this species has the dorsum covered with a few conical tubercles and 21 unipinnate branchial leaves.

Spaerodoris laevis was described by Bergh (1890) on the basis of a single specimen collected from Ambon, Indonesia. The preserved animal was described as being uniformly brown or olive gray with some yellowish areas on the dorsum. As described, the radula and reproductive system are identical to those of *Actinocyclus verrucosus*. Unfortunately, the holotype of this species is untraceable, and this synonymy is based on review of the original description.

Eliot (1913) described the new species *Spaerodoris japonica*, from Japan, which, in his opinion, might be conspecific with *A. verrucosus*. According to Eliot (1913), the main difference between *S. japonica* and other species of the genus is that both rhinophores open in the same cavity. However, Eliot recognized that this could be a teratology. He did not find other differences between both species that could justify the separation of *A. japonicus*.

Kay & Young (1969) redescribed *A. japonicus* from Hawaii, and regarded *Aldisa nhatrangensis* Risbec, 1956,

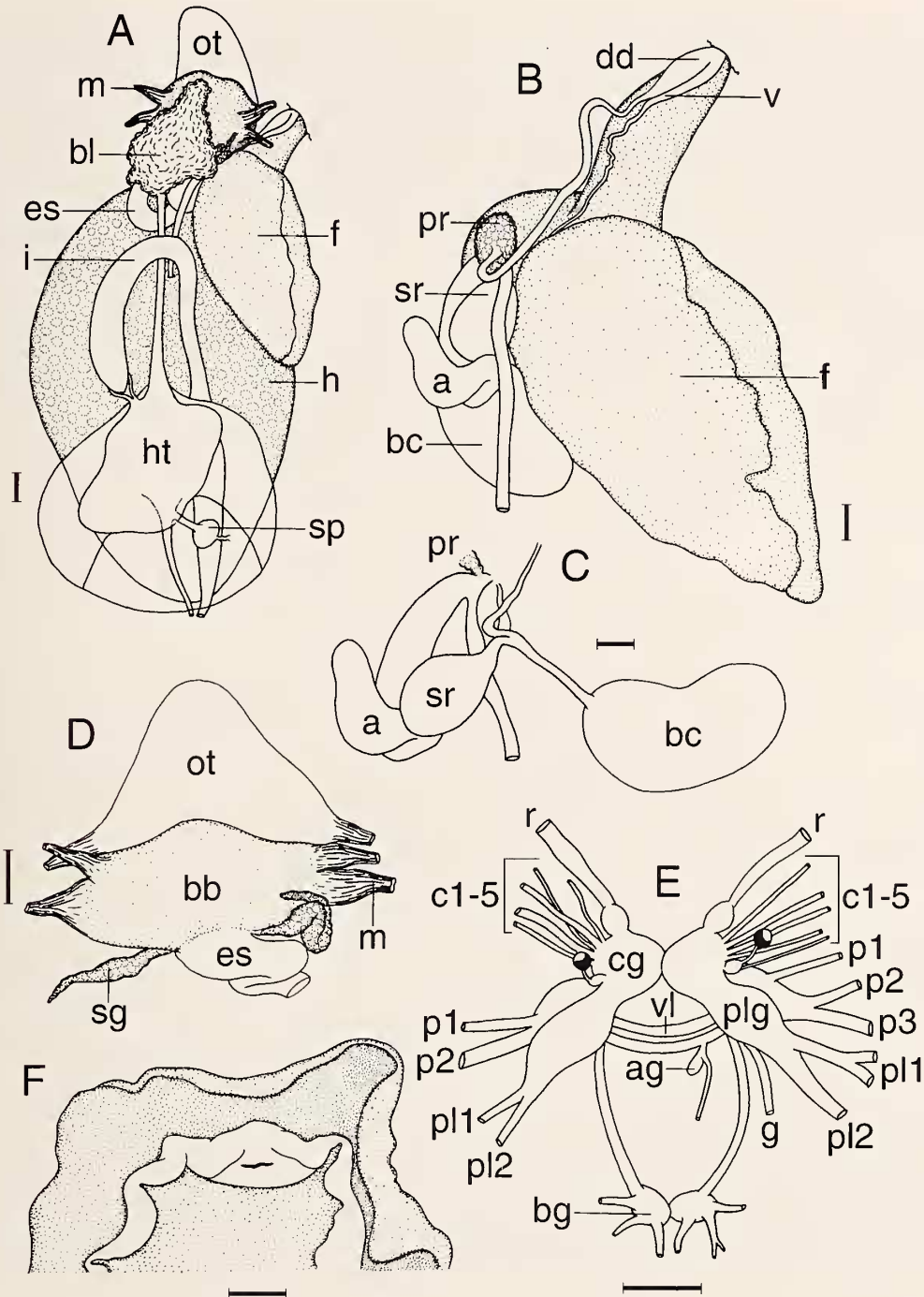


Figure 3. *Actinocyclus verrucosus*, anatomy of a specimen from Japan (CASIZ 099250). A. General view of the anatomy, scale bar = 1 mm. B. Reproductive system, scale bar = 1 mm. C. Detail of several reproductive organs, scale bar = 1 mm. D. Dorsal view of the buccal bulb, scale bar = 1 mm. E. Central nervous system, scale bar = 0.5 mm. F. Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: a, ampulla; ag, abdominal ganglion; bl, blood gland; bc, bursa copulatrix; bg, buccal ganglion; c, cerebral nerves; cg, cerebral ganglion; dd, deferent duct; es, esophagus; f, female glands; g, genital nerve; h, digestive gland; ht, heart; i, intestine; m, retractor muscles; ot, oral tube; p, pedal nerves; pl, pleural nerves; plg, pleural ganglion; pr, prostate; sg, salivary gland; sp, syrinx; rs, radular sac; sr, seminal receptacle; v, vagina; vl, visceral loop.

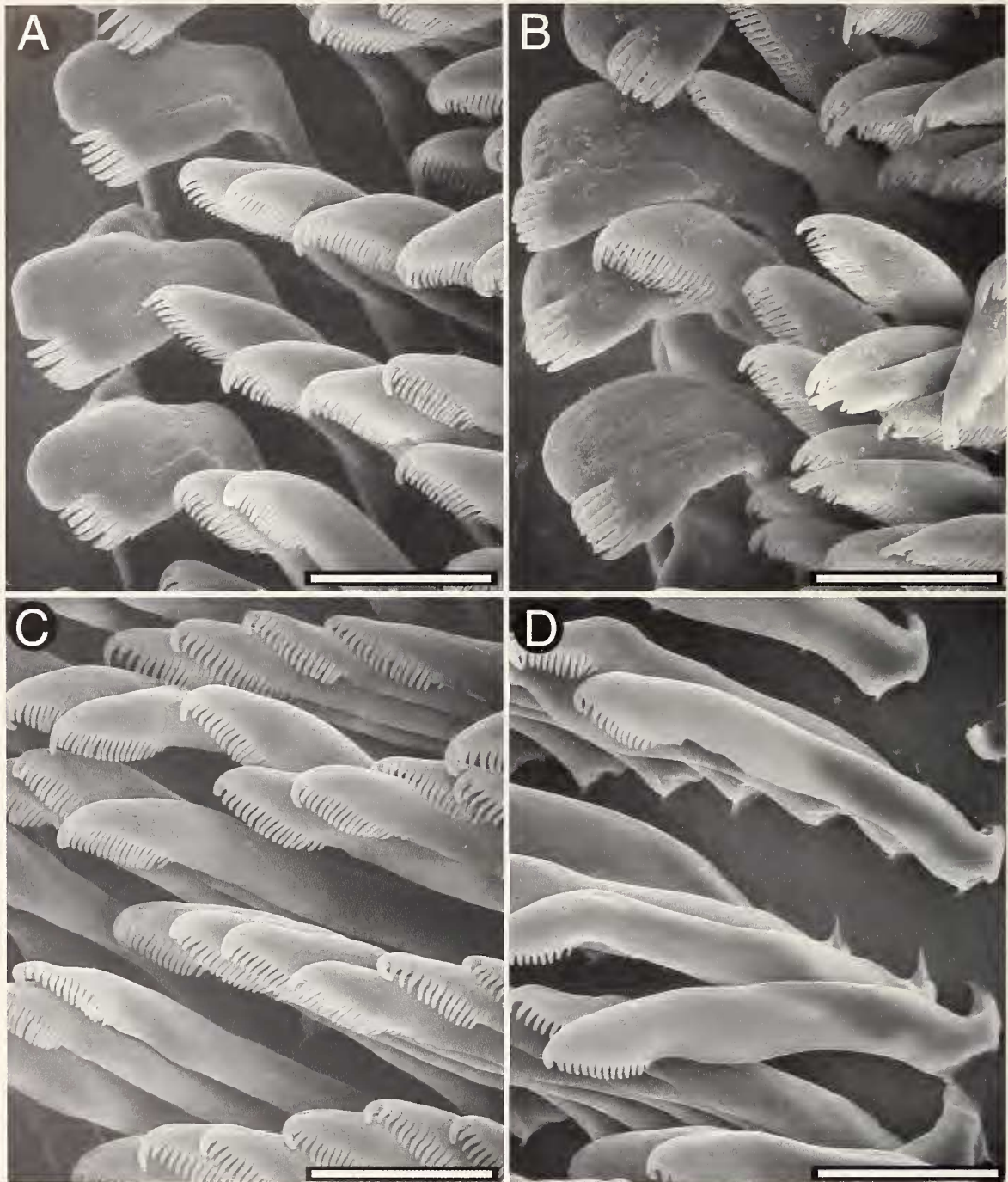


Figure 4. *Actinocyclus verrucosus*, scanning electron micrographs of the radula. A. Innermost lateral teeth of a specimen from Japan (CASIZ 099250), scale bar = 30 μm . B. Innermost lateral teeth of a specimen from Madagascar (CASIZ 073553), scale bar = 25 μm . C. Mid-lateral teeth of a specimen from Japan (CASIZ 099250), scale bar = 30 μm . D. Outermost lateral teeth of a specimen from Japan (CASIZ 099250), scale bar = 30 μm .

as a synonym. The radula and reproductive system are identical to those of our specimens.

After the examination of the type material of several species and additional specimens from Japan, the Philippines, Hawaii, and Madagascar, it is clear that *Actinocyclus verrucosus* is a widespread species in the tropical Indo-Pacific that exhibits wide variation in color, but also a great consistency in reproductive and radular features among different specimens.

There are two other species that were assigned to the genus *Actinocyclus* by Ehrenberg (1831), *Actinocyclus fragilis* Ehrenberg, 1831, and *A. velutinus* Ehrenberg, 1831. Both Bergh (1877) and O'Donoghue (1929) regarded them as unrecognizable. A re-examination of the original description of these taxa reveals that they do not belong to the genus *Actinocyclus* in the sense of its present usage. The dorsum of *A. velutinus* is covered with "very densely arranged minute hairs" (probably caryophyllidia), and *A. fragilis* is a large, yellowish brown species with densely arranged marginal dark spots and numerous dorsal tubercles.

Actinocyclus papillatus (Bergh, 1878)

(Figures 1C, 5,6)

Sphaerodoris papillata Bergh, 1877:66 (*nomen nudum*).
Bergh, 1878:590–592, pl. 66, figs 6,7.

Sphaerodoris laevis var. *variegata* Eliot, 1904:403–404.

Type material: *Sphaerodoris papillata* Bergh. Holotype (by monotypy): Ubay, Northwest of Bohol Island, Philippines, dissected (ZMUC GAS-2119). The holotype of *Sphaerodoris laevis* var. *variegata* is probably lost. It could not be located in the collections of The Natural History Museum, London (A. Campbell, personal communication).

Additional material: Barracuda Point, east side of Pig Island, near Madang, Papua New Guinea, 11 August 1989, 30 m depth, 1 specimen 35 mm preserved length, collected by M. Ghiselin (CASIZ 068651).

Geographic range: So far this species is known only from the east coast of Africa (Eliot, 1904), Japan (Hori & Fukuda, 1996), the Philippines (Bergh, 1878), and Papua New Guinea (this paper).

External morphology: The body is elevated, short and oval (Figure 1C). The dorsum is covered with numerous simple conical to rounded tubercles scattered irregularly. The tubercles situated on the center of the dorsum and near the gill opening are larger than the others. The central part of the body is clearly elevated over the mantle margin, which is relatively narrow. The perfoliate rhinophores are composed of 22 lamellae. There are 14 unipinnate branchial leaves in the 35 mm-preserved-length specimen. In the living animal they are pointing inward, with the apices very close to each other.

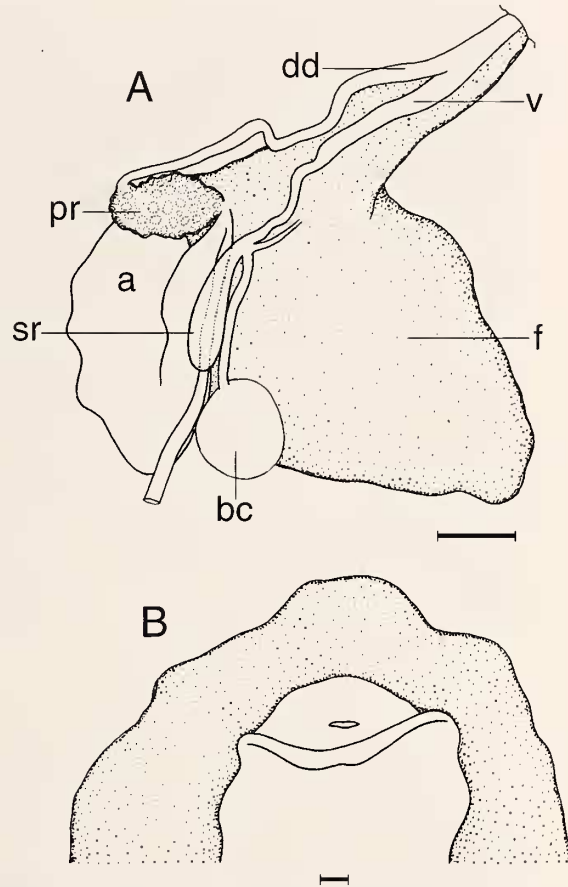


Figure 5. *Actinocyclus papillatus* (CASIZ 068651). A. Reproductive system, scale bar = 1 mm. B. Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: a, ampulla; bc, bursa copulatrix; dd, deferent duct; f, female glands; pr, prostate; sr, seminal receptacle; v, vagina.

The background color is reddish cream (Figure 1C). The entire dorsum is covered with a number of short, irregular, very densely arranged dark gray lines. Most of the lines are ramified into irregular branches. There are also irregular white areas, composed of the aggregation of numerous opaque white spots. The tubercles are pale brown or ochre, with the apex darker. A pale brown or ochre irregular line surrounds the mantle margin. The gill and rhinophores are pale brown to cream. The branchial leaves are covered with numerous minute white dots.

The anterior border of the foot is not grooved or notched, with anteriorly directed foot margins partially surrounding the mouth area (Figure 5B). There are no oral tentacles.

Anatomy: The jaws are composed of numerous, long undivided rodlets (Figure 6D). The radular formula is 69 × 29.0.29 in the 35 mm-preserved-length specimen (CASIZ 068651). Rachidian teeth are absent. The innermost lateral teeth are broad and elongate (Figure 6A). They have

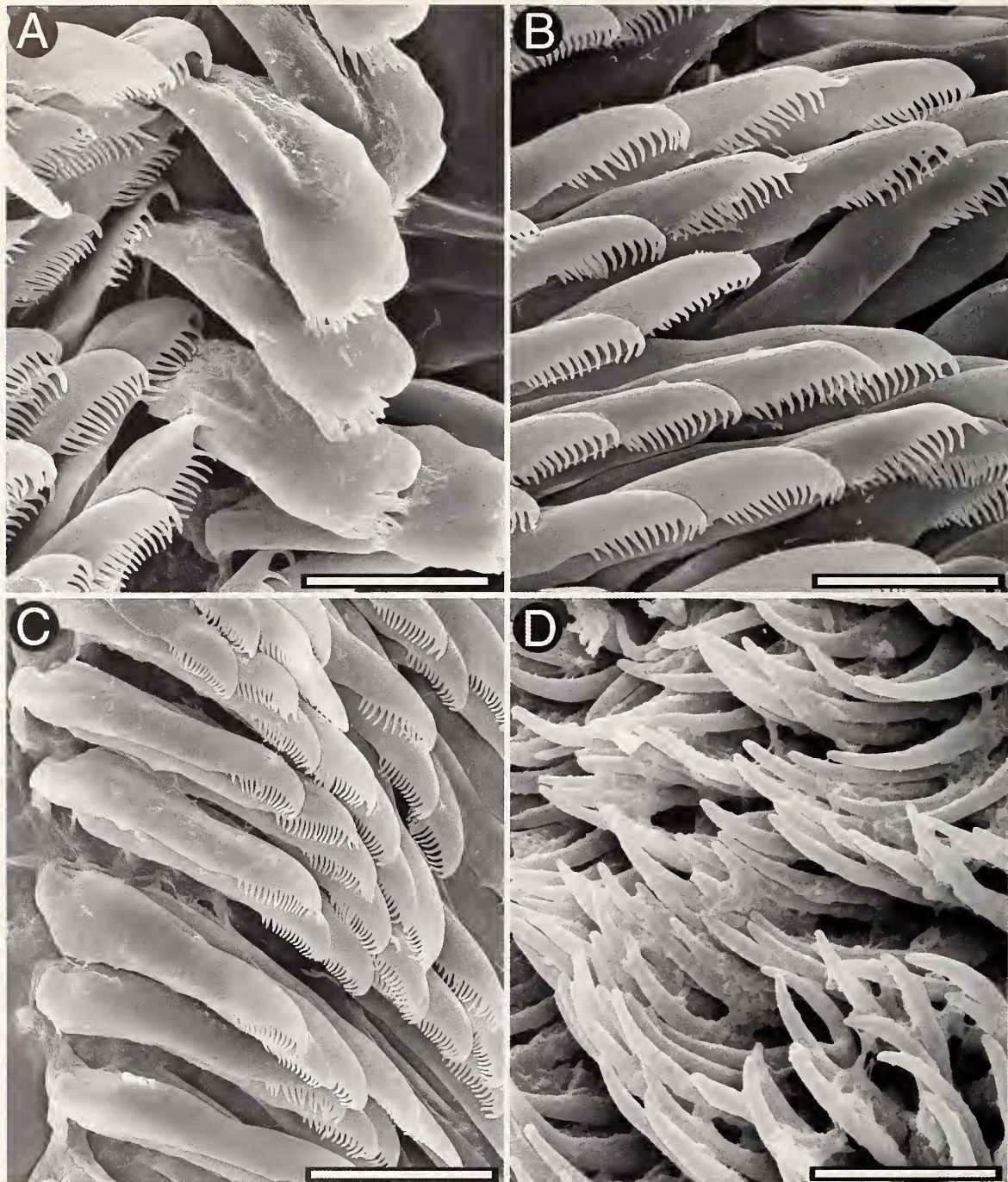


Figure 6. *Actinocyclus papillatus* (CASIZ 068651), scanning electron micrographs. A. Innermost lateral teeth, scale bar = 35 μm . B. Mid-lateral teeth, scale bar = 35 μm . C. Outermost lateral teeth, scale bar = 40 μm . D. Jaw elements, scale bar = 10 μm .

a very short and wide rounded cusp and six to eight elongate denticles along their inner edge. The mid-lateral teeth have a narrow base and are elongated (Figure 6B). They are also multidenticulated, with 12–16 long denticles. The outermost teeth are shorter than the mid-laterals,

but very similar in shape (Figure 6C). The outer laterals have 12–16 denticles along their inner margin.

The narrow hermaphroditic duct expands into the large ampulla, which inserts distally at the junction of the oviduct and the prostate (Figure 5A). The oviduct enters the